# Carbon and nitrogen loss rates during aging of lake sediment: Changes over 27 years studied in varved lake sediment

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Abstract

We used a collection of ten freeze cores of annually laminated (varved) lake sediment from Nylandssjön in northern Sweden collected from 1979 to 2007 to follow the long-term loss of carbon (C) and nitrogen (N) due to processes that occur in the lake bottom as sediment ages. We compared specific years in the different cores. For example, the loss of C from the surface varve of the 1979 core (sediment deposited during 1978) was followed in the cores from 1980, 1985, 1989, and so on until 2006. The C concentration of the sediment decreased by 20% and N decreased by 30% within the first five years after deposition, and after 27 yr in the sediment, there was a 23% loss of C and 35% loss of N. Because the relative loss of C with time was smaller than loss of N, the C:N ratio increased with increasing age of the sediment; the surface varves start with a ratio of ~10, which then increases to ~12.

Knowledge of carbon (C) and nitrogen (N) turnover and sequestration in lake sediment is important for a number of reasons, including lake management related to eutrophication, C budgets related to global warming, and, for paleolimnology to improve understanding of sediment deposits as archives for inference of past environmental conditions. Early sedimentary diagenesis has been studied in laboratory incubation experiments on freshwater algae (e.g., Foree and McCarty 1970; Jewell and McCarty 1971; Lehman et al. 2002) as well as marine algae (e.g., Emerson and Hedges 1988; Harvey et al. 1995; Kristensen and Holmer 2001). These experiments, which typically have been conducted over a period of weeks up to a year, have reported high decay rates and a large variability, spanning over three orders of magnitude; the reason for this is assumed to be differing algal material, incubation temperatures, and the use of single- versus double-exponential decay models (Lehman et al. 2002). Besides laboratory experiments, there have been a number of studies in lakes with oxic hypolimnion, where sediment trap accumulation rates were compared to sediment core accumulation rates, i.e., sediment traps were emptied weekly, biweekly, or at slightly longer intervals, and the cumulative sedimentation rates from the traps were compared to the net annual or seasonal accumulation rates found in sediment cores (Hamilton-Taylor and Willis 1984; Jonsson and Jansson 1997; Teranes and Bernasconi 2000). These studies reported loss rates for C of 25–45% and for N of 40–70% after 1–3 yr. Lehmann et al. (2002) did a similar study in seasonally anoxic Lake Lugano, and the net loss of C was 15–20%. Hodell and Schelske (1998) compared two sediment cores taken six years apart from the same location in Lake Ontario. Although that study focused on changes in the isotopic composition of C by diagenetic processes, it can be estimated from their data that 20–30% of the C was lost from the sediment.

Thus, previous studies have mainly looked at initial degradation processes of organic material, i.e., remineralization taking place within days, weeks, months, or years after deposition. In this study, we analyzed a series of 10 freeze cores, collected at irregular intervals from 1979 to 2007, made up of annually laminated (varved) sediments to determine the loss rate with time of C and N from the sediment over a 27-yr-long period. Unlike common lake sediments, which are mixed and require dating by radiometric methods that involve a degree of uncertainty, the varves provide an accurate timescale. The cores were stored intact in a freezer room from coring until they were subsampled and analyzed in 2004–2007. This core series allowed us to determine how the C and N content of individual varves changed with time. We did this by comparing the elemental composition of given years (varves) in the different cores that were stored in the freezer room. For example, the C content of the varve that was deposited in 1978 (the surface varve in the 1979 core) can be followed in the cores sampled in 1980, 1985, 1989, and so on, until 2006. These data provide a unique opportunity to follow the progressive influence of diage-

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netic processes on sediment when it is aging in the lake bottom. The time window we studied was from 0.5 to 27 yr after sediment deposition.

## Material and methods

Study site—Nylandssjön (62°57′N, 18°17′E) is a dimictic boreal forest lake located at the coast of the Gulf of Bothnia in northern Sweden. The lake surface area is 0.28 km<sup>2</sup>, and the catchment area is 0.95 km<sup>2</sup>. The lake has only a few very small inlets during snowmelt in spring and during periods of continuous rain. The mean annual precipitation is 800 mm, and the mean annual air temperature is 4°C. The landscape has a broken topography; valleys are used for cultivation and pasture, and hills are covered with Norway spruce, Scots pine, and birch. About 15% of the catchment area of the lake is arable land. The lake has two deep basins, 17.5 and 14.3 m deep. In the deeper basin, varve formation started after isolation of the lake from the sea by land upheaval about 3,400 yr ago. With time, the varve quality deteriorated, and by the nineteenth century, varve formation had ceased. At the beginning of the twentieth century, varves started to form again due to cultural eutrophication (Renberg 1986). Nylandssjön is a circumneutral, soft-water lake (calcium concentration in the water is 0.1 mmol  $L^{-1}$ ), it has a phosphorus concentration of about 20  $\mu$ g L<sup>-1</sup>, and regular oxygen depletion occurs in the hypolimnion in summer and in winter, which is a prerequisite for varve formation. During the last several decades, very distinctive varves have been deposited. For further details about the lake, see Petterson et al. (1993) and Gälman et al. (2006). Both autochthonous and allochthonous material sources contribute organic material to Nylandssjön. The atomic C:N ratio from 3 yr of sediment trap studies (Gälman unpubl.) shows a minimum of 8, a maximum of 15, and an average of 11. Since plankton and bacteria usually have C:N ratios that range from 5 to 8 (Meyers 1994), and terrestrial organic matter ratios range from 20 to 100 (Jasper and Gagosian 1989), ~70\% of the organic material in Nylandssjön sediment is of autochthonous origin.

Varved lake sediment—At the sediment—water interface, the varves are about 1 cm thick, and by compaction and remineralization of organic material, the varves become thinner with time and are typically about 2–3 mm in 50-yrold sediment (the water content decreases from 96–98% to 86–87% of the wet mass). For the last 30-yr period, the net dry mass accumulation rate of sediment has been ~30 mg cm<sup>-2</sup> yr<sup>-1</sup>, of which 20 mg cm<sup>-2</sup> yr<sup>-1</sup> is minerogenic matter (autochthonous and allochthonous minerals), 5 mg cm<sup>-2</sup> yr<sup>-1</sup> is biogenic silica, 4 mg cm<sup>-2</sup> yr<sup>-1</sup> is carbon,  $0.4 \text{ mg cm}^{-2} \text{ yr}^{-1}$  is nitrogen,  $1.5 \text{ mg cm}^{-2} \text{ yr}^{-1}$  is iron, and the calcium accumulation rate is low (0.2 mg cm<sup>-2</sup>  $yr^{-1}$ ; no calcium carbonate precipitation). The most distinctive feature of a varve is the thin dark winter layer (Fig. 1), but other seasonal layers are also discernible by the naked eye, but particularly in thin sections (Renberg 1981a). Unlike the varve thickness, the internal structure

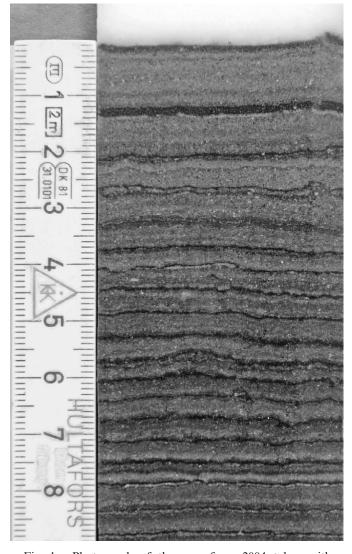


Fig. 1. Photograph of the core from 2004 taken with a standard digital camera in the freezer room after cleaning of the core surface. The distinct, thin darker layers are the winter layers. The white material above the topmost winter layer is frozen water. The ruler is in cm.

and color of the varves do not change with time, and it is easy to match cores taken from different years and to identify the individual varves (Renberg 1986; Gälman et al. 2006). Formation processes of this type of sediment were outlined by Renberg (1981*a*).

Sediment sampling and subsampling—Sediment cores were taken using a freeze corer (Renberg 1981b). Immediately after a core was detached from the sampler in the field, the still-frozen core was wrapped in a black plastic bag, transported frozen to the laboratory, and stored in a freezer room at  $-18^{\circ}$ C. Cores were taken in late winter (March–April) from lake ice. The cores used in this study were taken in 1979, 1980, 1985, 1989, 1993, 1997, 2002, 2004, 2006, and 2007. Because the cores were taken in winter when sediment deposition is minute, the uppermost

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varve represents sediment deposited during the previous year, i.e., in the 2007 core, the surface varve is the sediment deposited in 2006.

Subsampling followed Renberg (1981b). The corer produces two flat slabs of frozen sediment, one from each flat rectangular side of the sampler, and only one slab was used here. The subsampling took place in a freezer room. It involved cleaning of all sides of the slab with a woodworker's hand plane. After cleaning, digital photographs were taken for documentation, and then individual varves were cut and scraped off with a steel scalpel. The upper surface of the thin, black, winter layer (formed during the period November–April) was used as the division between years. The thick surface varves were easy to subsample accurately, but due to sediment compaction and declining varve thickness, in practice, it was difficult to subsample individual varves older than 35 yr in each core with high accuracy. The data set includes >300 individual samples spanning the period from 1950 to 2006. The core from 2007 was only subsampled to 1984.

Analyses—Samples were freeze dried, the water content was determined, and the C and N concentrations were analyzed with a Perkin Elmer 2400-CHNS/O elemental analyzer, operated in CHN mode. Analytical quality was verified against certified standard material (LKSD-4 from National Resources Canada, lake sediment sample CCRMP from CANMET Mining and Mineral Sciences) and internal standards. Replicate samples for C and N were within 0.8% and 1.1% relative standard error (RSE). Concentrations of C and N are expressed as percent of the dry sediment mass. The C:N ratio is given as the atomic ratio.

Calculations of C and N loss rates with time—The basic approach to assess the loss rates of C and N with time is graphical. The loss rate with time was calculated as a percent of the concentration of the original surface varve. For example, the loss of the 1978 varve (surface varve in 1979 core) after one year was calculated using the core from 1980, the loss after 6 vr was calculated using the core from 1985, etc. A restricted maximum likelihood method was used to fit models to the changes in C and N data over time, using the mixed-model module in the statistical software package SPSS 14.0 (SPSS Inc.). Independence was assumed between loss data from different surface varves. A linear relationship between changes and t/(t+1), where t is the number of years in the sediment, was estimated for the individual surface varves (treated as a random effect) and for all surface varves together (a general relationship). The model assumed a homogeneous first-order autoregressive dependence structure for the residuals within surface

For comparison, we also applied our data to the G model (Westrich and Berner 1984), and for this, we used nonlinear least squares regression and applied both the relative loss rates and recalculated C and N concentrations (where starting concentrations were set to the average of all surface varves). These two approaches gave the same results in terms of exponential rate coefficients.

#### Results

Independently of what year a core was sampled, the C and N contents of the varves are highest near the sediment surface and decline downward in the core (Fig. 2a,b). This is the result of C and N loss from the sediment with time. In Fig. 3a,b, the surface varve of the different cores was followed in subsequent cores, e.g., the varve deposited in 1978 was followed in the core taken in 1980 (after 1 yr), in 1985 (after 6 yr), and the other cores until 2006, and the loss of C and N, in percent of the 1978 year's varve, was calculated and plotted against time. The loss rate is largest during the first five years, about 20% for C and 30% for N. The loss curves then flatten out to ~23% for C and 35% for N after 27 yr (Fig. 3a,b). The relative loss of C (Eq. 1) and N (Eq. 2), respectively, can be described with the following equations:

$$C_{loss} = 23.41t/(t+1)$$
  
(SE = 1.17, p = 0.000) (1)

$$N_{loss} = 36.17t/(t+1)$$
  
(SE = 1.09, p = 0.000) (2)

where t is the number of years in the sediment, and SE is the standard error.

The relative loss rate of C with time is smaller than that for N, which is manifested by an increasing C:N ratio with increasing age of the sediment. The surface varves start with a ratio of 9.5 to 10.5 and increase with age to 11.5 to 12.5 (Fig. 3c).

The temporal trends in C and N contents of the sediment from 1950 to 2006 in Fig. 2a,b are also influenced by a flux rate maximum of organic matter (data not shown) in the mid-1990s caused by eutrophication of the lake. That is a separate issue and is not considered further in this paper. One fact worth considering however, is the similarity of the year-to-year variations of the C and N contents, respectively, in different cores (Fig. 2a,b), which are related to annual productivity changes in the lake and to catchment disturbances.

### Discussion

The downcore patterns of the C and N contents of the older, consolidated varve sections are similar, independent of the year the cores were collected. This is a strong indication for the high accuracy of the data set. There are individual years that do have differences in concentrations of C and N between cores (Fig. 2a,b). This variability is a combined effect of subsampling and analytical errors and also small-scale spatial variability in sediment accumulation over the lake bottom. The cores were not taken at exactly the same location in the 17.5-m-deep basin because coring spots were determined using an echo sounder to find the deepest area in the basin, and differences on a decimeter-scale in water depth are important for the sediment accumulation rate (Petterson et al. 1993; Gälman et al. 2006). Besides that, it is likely that sediment

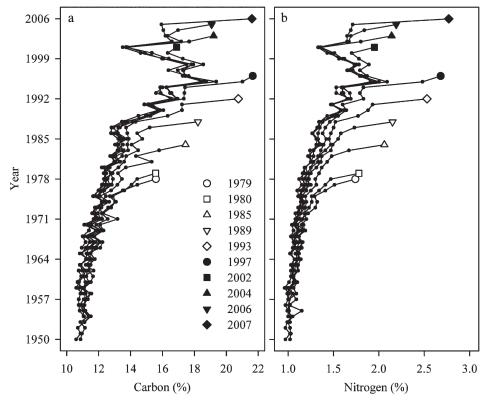


Fig. 2. (a) C and (b) N concentrations (percent of dry sediment mass) of the individual varves of the 10 sediment cores plotted against calendar years.

constituents such as mineral grains, coarse organic particles, and even remains of diatoms and other algae are not evenly deposited on the lake bottom, as seen on a microscale, and it is possible that this uneven sedimentation is accentuated by a slightly undulating bottom surface caused by distortion from fish and from human activities, including sediment coring, over the years. The small-scale year-to-year differences that can be seen in the C and N record (Fig. 2a,b) are preserved in the sediment despite clear evidence of in situ diagenesis. This fact strengthens the value of organic matter as a paleoproductivity proxy, particularly considering that diagenesis diminishes markedly after five years.

Loss rates of C and N are high during the first several years and decrease with time (Fig. 3a,b), and the loss rates can be described well with Eqs. 1 and 2 (p = 0.000). The curves generated from Eqs. 1 and 2 are very similar to the ones based on the G model (Fig. 4a,b). Equations 1 and 2 show that five years after deposition, ~20% of the C and 30% of the N are lost, and after 27 yr, ~23% and 35% are lost, respectively. At the end of the 27-yr period covered by our core sequence, the trends in the sediment may still be declining (Fig. 3a,b), particularly the N curve, but the analytical uncertainty of the data and the fact that there are no older cores to compare with, do not allow any firm conclusions. The loss rate of N from the sediment is about 33% larger than for C in recent sediment (0–3 yr), which is a bit lower than the values previous studies using sediment traps have found of 36-41% (Hamilton-Taylor and Willis 1984; Jonsson and Jansson 1997; Teranes and Bernasconi 2000). This can be explained by different starting times of the experiments (see following discussion), and differing oxygen regimes. In Nylandssjön, the accumulation rate of C and N, respectively, is typically 5 and 0.8 mg cm<sup>-2</sup> yr<sup>-1</sup> in the deep basin (in the surface varves), and of this, about 1.1 and 0.2 mg cm<sup>-2</sup> yr<sup>-1</sup> is recycled to the lake, while 3.9 and 0.6 mg cm<sup>-2</sup>yr<sup>-1</sup> is sequestrated (27 yr later).

The increase in C:N ratio with age (Fig. 3c) is expected because of bacterial preference for degradation of N-rich compounds (Fenchel et al. 1998). Also, newly deposited sediment contains easily degradable material from algae and has a C:N ratio of 6–8 (Meyers and Ishiwatari 1993; Meyers and Teranes 2001; Talbot 2001), and when this material is degraded, the relative influence of more resistant terrestrial material with a higher ratio becomes larger, leading to a higher C:N ratio of the sediment with time. However, the increase in C:N ratio can be reduced by bioremineralization due to input of low C:N bacterial biomass (e.g. Müller 1977; Lehmann et al. 2002).

When the diagenetic loss rates of C and N in Nylandssjön are compared with results of other studies, several factors must be considered, such as (1) the time window studied on the path of the sediment material, from being newly deposited on the lake bottom to the final stage many years later when the material is preserved without measurable change, (2) the initial composition of the sediment material, (3) the importance of anoxic versus oxic conditions, and (4) sediment mixing, fragmentation, and consumption by benthic invertebrates.

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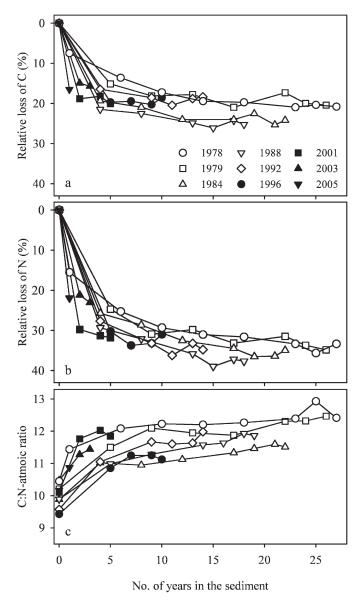


Fig. 3. Curves illustrating the relative loss of (a) C and (b) N with time. The diagrams were constructed in the following way: The C and N concentration, respectively, of the surface varve for each core was followed in subsequent cores, and the loss of C and N of this surface varve in each subsequent core was calculated relative to the surface varve (expressed as percent). For example, the varve deposited in 1978 (1979 core) was followed in the core taken in 1980 (loss after 1 yr), in the core taken in 1985 (loss after 6 yr), and in subsequent cores until 2006. The *x*-axis represents the number of years the surface varve has been in the sediment. (c) The C: N ratio of the surface varves was followed in the same way in subsequent cores, and the C: N ratio is plotted against time in the sediment.

The surface material in Nylandssjön was about half a year old at the time of coring, because sediment deposition largely ceases in October, and cores were taken in March–April the following year. This means that a considerable amount of the most easily degradable organic material had already been remineralized. Given that, it is logical for incubation studies with a short duration to indicate much

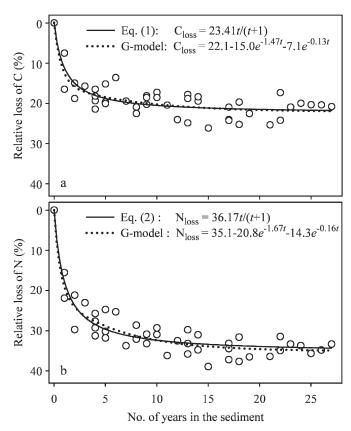


Fig. 4. Degradation curves based on Eqs. 1 and 2, and the G model by Westrich and Berner (1984), illustrating the loss of (a) C and (b) N with time, using percent data.

higher loss rates. If we apply our data (Fig. 3a,b) to the double-exponential decay equation (Westrich and Berner 1984), we confirm this assumption. This so-called G model, which is a widely used decay model in aquatic and marine studies, yields a degradation rate coefficient  $(k_1)$  for the more labile organic matter fraction and a second coefficient  $(k_2)$  for the slowly decaying fraction. Our data set gives kvalues that are very low—for C,  $k_1 = 1.47$  and  $k_2 = 0.134$ , and for N,  $k_1 = 1.67$  and  $k_2 = 0.166$ —while incubation experiments typically find higher k values (Harvey et al. 1995; Kristensen and Holmer 2001; Lehmann et al. 2002). Our  $k_1$  values are about the same size as the  $k_2$  values from the anoxic incubation experiments (with sulfate) of Kristensen and Holmer (2001) and Lehmann et al. (2002), which is interesting because Nylandssjön has anoxic conditions in the hypolimnion, except for short periods at overturn in spring and autumn (Gälman unpubl.), and the degradation of organic material is probably mediated by reduction of Mn, Fe, NO<sub>3</sub><sup>-</sup>, SO<sub>4</sub><sup>2-</sup>, and methanogenesis.

The importance of the initial composition of the sediment material is illustrated by the fact that the loss rates for C and N vary somewhat between different varve years (Fig. 3a,b). The loss rate after, for example, 10 yr is about 5% larger in the varves that were deposited in 1984 (surface varve in 1985 core) and 1988 (1989 core) as compared to the varves that were deposited in 1978 (1979 core) and 1979 (1980 core). The differences in initial

composition of the organic matter can be caused by variations in the nutrient supply to the lake, which will facilitate different algae communities, as well as differences in the proportion of allochthonous material.

The influence of oxic versus anoxic conditions on the degradation rate of organic material has been widely discussed, and research has shown contradictory results. A number of incubation experiments have shown that for the most reactive organic material, the degradation rate is the same in oxic and anoxic conditions (Andersen 1996; Kristensen and Holmer 2001; Lehman et al. 2002), but already degraded organic material has a slower decomposition rate in anoxic conditions (Meyers and Ishiwatari 1993; Kristensen and Holmer 2001; Lehman et al. 2002). Lehmann et al. (2002) compared C and N in surface sediment varves to sediment accumulation rates in sediment traps in eutrophic, seasonally anoxic Lake Lugano, which had a net loss of 30–40% organic matter over 0–3 yr. Converted to organic C (dividing organic matter by a factor of 2; Håkanson and Jansson 1983), the net loss of C was 15-20%. Teranes and Bernasconi (2000) did a similar study in varved, eutrophic Baldeggersee, which has been artificially aerated since 1982 to reduce hypolimnetic anoxia. Core-top accumulation rates per seasonal layer were compared to total seasonal sediment trap accumulations, and net loss of C was 25–28%. This is an  $\sim 30\%$ higher net loss of C in the oxic lake than in the seasonally anoxic Lake Lugano.

Hodell and Schelske (1998) compared two sediment cores collected six years apart in oxic Lake Ontario. The difference in accumulation rates of organic C (mg cm<sup>-2</sup>  $yr^{-1}$ ) of the surface sediment collected in 1987 and the same estimated year from the core collected in 1993 is about 20– 30%, which is a bit higher than in Nylandssjön (20% after 6 yr). A factor to consider when comparing the results from Lake Ontario and Nylandssjön is that the sediment from Nylandssjön can be dated with a high accuracy because the sediment is varved, while in Lake Ontario, the cores were dated using 210Pb and 137Cs, which gives less accurate dating. Another aspect to consider is that Lake Ontario has calcite precipitation in the form of whiting events, when calcite crystals aggregate with phytoplankton algae and bacteria, which might lead to rapid sedimentation and reduced remineralization in the water column (Hodell and Schelske 1998; Dean 1999). This can mean that lakes with CaCO<sub>3</sub> precipitation, in the form of whiting events, can receive a higher proportion of easily degradable organic material to the sediment than lakes without the effect of a more rapid delivery system through the water column to the sediment, i.e., a higher proportion of easily degradable organic material can give a higher decomposition rate.

The sediment in the deep basin of Nylandssjön, where our study was performed, is not mixed by water movements or benthic fauna. This is a prerequisite for varve formation. The sediment is therefore not typical for most lakes. It is possible that the lack of mixing slows down the decay process. Studies of the effects of bioturbation on lake sediments suggest that mixing is an important factor (Aller 1994; Kristensen 2000; Stief 2007). The ideal design setup

to study this would be a comparative study in a lake with both a basin with varved sediment and a basin with mixed sediment.

This study, which is the first empirical assessment of long-term effects of lake sediment degradation of organic matter, shows that a substantial part of both C and N is sequestrated in the sediment in the time window from 0.5 to 27 yr after deposition. This data set cannot be used to draw any conclusions about the initial degradation (time window 0–0.5 yr), when a large part of the material is remineralized and recycled to the lake water. A major part of the C and N loss from the sediment occurs within 5 yr after deposition (20% and 30%, respectively). After that, the loss rate is low, and the year-to-year similarity of the C and N contents of the different cores is a clear indication that the organic matter concentration of the consolidated varve sediment deposit reflects the initial accumulation of organic matter on the lake bottom. This is an important prerequisite for paleolimnological investigations of environmental change, e.g., eutrophication, climate influence, etc. On the other hand, this study clearly demonstrates that diagenetic processes change the C:N ratio of sediment with time and confirms that the decline in the C:N ratio that has been observed in near-surface sediments in several paleolimnological investigations can be a process artifact and should not be uncritically interpreted as a shift over time in the proportion of organic matter from different sources, such as increased influx of algae or less influx of organic material from terrestrial plants (which have a high C:N ratio).

# References

ALLER, R. C. 1994. Bioturbation and remineralization of sedimentary organic matter: Effects of redox oscillation. Chem. Geol. 114: 331–345.

Andersen, F. Ø. 1996. Fate of organic carbon added as diatom cells to oxic and anoxic marine sediment microcosms. Mar. Ecol. Prog. Ser. 134: 225–233.

DEAN, W. E. 1999. The carbon cycle and biogeochemical dynamics in lake sediments. J. Paleolimnol. 21: 375–393.

EMERSON, S., AND J. I. HEDGES. 1988. Processes controlling the organic carbon content of open ocean sediments. Paleoceanogr. 3: 621–634.

FENCHEL, T., G. M. KING, AND T. H. BLACKBURN. 1998. Bacterial biogeochemistry: The ecophysiology of mineral cycling. Academic Press.

Foree, E. G., and P. L. McCarty. 1970. Anaerobic decomposition of algae. Environ. Sci. Technol. 4: 842–849.

Gälman, V., G. Peterson, and I. Renberg. 2006. A comparison of sediment varves (1950–2003 AD) in two adjacent lakes in northern Sweden. J. Paleolimnol. 35: 837–853, doi:10.1007/s10933-005-5925-x.

HÅKANSON, L., AND M. JANSSON. 1983. Principles of lake sedimentology. Springer-Verlag.

Hamilton-Taylor, J., and M. Willis. 1984. Depositional fluxes of metals and phytoplankton in Windermere as measured by sediment traps. Limnol. Oceanogr. **29:** 695–710.

HARVEY, H. R., J. H. TUTTLE, AND J. T. BELL. 1995. Kinetics of phytoplankton decay during simulated sedimentation: Changes in biochemical composition and microbial activity under oxic and anoxic conditions. Geochim. Cosmochim. Acta 59: 3367–3377. 1082 Gälman et al.

HODELL, D. A., AND C. L. SCHELSKE. 1998. Production, sedimentation, and isotopic composition of organic matter in Lake Ontario. Limnol. Oceanogr. 43: 200–214.

- Jasper, J. P., and R. B. Gagosian. 1989. Glacial-interglacial climatically forced  $\delta^{13}C$  variations in sedimentary organic matter. Nature **342**: 60–62.
- Jewell, W. J., and P. L. McCarty. 1971. Aerobic decomposition of algae. Environ. Sci. Technol. 5: 1023–1031.
- JONSSON, A., AND M. JANSSON. 1997. Sedimentation and mineralization of organic carbon, nitrogen and phosphorus in a large humic lake, northern Sweden. Arch. Hydrobiol. 141: 45–65.
- Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in costal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia **426**: 1–24.
- ——, AND M. HOLMER. 2001. Decomposition of plant materials in marine sediment exposed to different electron acceptors (O<sub>2</sub>, NO<sub>3</sub><sup>-</sup>, and SO<sub>4</sub><sup>2</sup>), with emphasis on substrate origin, degradation kinetics, and the role of bioturbation. Geochim. Cosmochim. Acta **65**: 419–433.
- Lehmann, M. F., S. M. Bernasconi, A. Barbieri, and J. A. McKenzie. 2002. Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. Geochim. Cosmochim. Acta 66: 3573–3584.
- MEYERS, P. A. 1994. Preservation of elemental and isotopic source identification of sedimentary organic-matter. Chem. Geol. **114:** 289–302.
- ——, AND R. ISHIWATARI. 1993. Lacustrine organic geochemistry—an overview of organic matter sources and diagenesis in lake sediments. Org. Geochem. **20:** 867–900.
- ——, AND J. L. TERANES. 2001. Sediment organic matter, p. 239–269. *In* W. M. Last and J. P. Smol [eds.], Tracking environmental change using lake sediments. Vol. 2. Kluwer.

- Müller, P. J. 1977. C/N ratios in deep-sea sediments: Effects of inorganic ammonium and organic compounds sorbed by clays. Geochim. Cosmochim. Acta 41: 549–553.
- Petterson, G., I. Renberg, P. Geladi, A. Lindberg, and F. Lindgren. 1993. Spatial uniformity of sediment accumulation in varved lake sediments in northern Sweden. J. Paleolimnol. 9: 195–208.
- Renberg, I. 1981a. Formation, structure and visual appearance of iron-rich, varved lake sediments. Verh. Int. Ver. Limnol. 21: 94–101.
- ——. 1981b. Improved methods for sampling, photographing and varve-counting of varved lake sediments. Boreas 10: 255–258.
- . 1986. Photographic demonstration of the annual nature of a varve type common in N. Swedish lake sediments. Hydrobiologia 140: 93–95.
- STIEF, P. 2007. Enhanced exoenzyme activities in the presence of deposit-feeding *Chironomus riparius* larvae. Freshw. Biol. 52: 1807–1819.
- TALBOT, M. R. 2001. Nitrogen isotopes in palaeolimnology, p. 401–439. In W. M. Last and J. P. Smol [eds.], Tracking environmental change using lake sediments. Vol. 2. Kluwer.
- Teranes, J. L., and S. M. Bernasconi. 2000. The record of nitrate utilization and productivity limitation provided by  $\delta^{15}N$  values in lake organic matter—a study of sediment trap and core sediments from Baldeggersee, Switzerland. Limnol. Oceanogr. 45: 801–813.
- Westrich, J. T., and R. A. Berner. 1984. The role of sedimentary organic matter in bacterial sulfate reduction: The G model tested. Limnol. Oceanogr. 29: 236–249.

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